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**Research Paper
RM-301**

Effect of Prolonged Drought on Water Relations of Ponderosa Pine Seedlings Growing in Basalt and Sedimentary Soils

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Abstract

This study compared the effects of prolonged drought on container and bare-root ponderosa pine seedlings growing in sedimentary and basalt soils. Seasonal and diurnal responses were compared. Upon rewatering, transpiration and needle water potential of stressed seedlings recovered quite rapidly while stomatal conductance recovered less rapidly. There was little difference in performance between container and bare-root seedlings. In cases of severe drought, however, survival will probably be higher on basalt soils because of their greater water-holding capacity.

[1]Headquarters is in Fort Collins, in cooperation with Colorado State University; research reported here was conducted at the Station's research work unit in Flagstaff, in cooperation with Northern Arizona University.

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L. J. Heidmann and Rudy M. King

Ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelm.) is the predominant timber species in the southwestern United States (Schubert 1974). Although total precipitation in the region (from less than 35 to more than 100 cm annually) is adequate for tree growth, periods of drought during the spring make seedling establishment difficult. The effects of drought are accentuated by competing herbaceous vegetation (Schubert et al. 1970, Heidmann et al. 1977).

Establishment of ponderosa pine regeneration is directly related to soil type. The forest soils of the southwestern United States are either sedimentary or volcanic in origin (Heidmann 1975). Fine-textured volcanic soils, which are derived from basalt rocks, are composed primarily of silt and clay. Although these soils have more available water than coarser sedimentary soils, water becomes limiting when soil moisture content (SMC) drops below 10%. In sedimentary soils, water becomes limiting to seedlings below 1.5% SMC. Natural regeneration is much easier to establish on sedimentary soils despite its lower water-holding capacity, primarily because first-year seedlings are larger and more vigorous. On basalt soils, first-year natural seedlings are very small and frost heave at an excessive rate (Heidmann 1975). In addition, small seedlings desiccate very rapidly.

Bare-root and container seedlings have been planted successfully on both soils in the past; however, bare-root seedlings have been more difficult to establish, possibly because of smaller root systems. Container seedlings have more extensive root systems which are planted intact. A large root system and a relatively small top appear to be advantageous to establishment of ponderosa pine seedlings (Heidmann 1988). Container planting programs are more flexible because seedlings may be planted in the spring or fall when seedlings are dormant or during the summer when actively growing. Bare-root seedlings, however, must be planted in the early spring or the late fall when seedlings are dormant. Thus, periods of drought almost always follow planting of bare-root seedlings; but if container seedlings are planted during the summer, moisture is plentiful.

Although ponderosa pine is a drought-tolerant species, the effect of prolonged water stress on seedling physiology has not been studied. In this study we wanted to determine if the effects of prolonged drought on ponderosa pine seedlings varied by soil type. In addition, we wanted to know if container and bare-root seedlings responded differently to drought on the two soils. Finally, we were interested in studying seedling responses to drought during the fall and during late spring and early summer, the most common times for planting seedlings. Consequently, a study to determine the effects of prolonged drought on ponderosa pine seedlings growing in sedimentary and basalt soils was begun in 1984. Transpiration (E) and stomatal conductance (gs), needle water potential (ψ_ℓ), soil moisture content (SMC), and soil water potential (ψ_s) data were compared for seedlings that had set terminal buds and were entering dormancy in the fall, and seedlings during the following summer growing season.

Methods

Soils

Soils were obtained from two sites in the ponderosa pine ecosystem. Sedimentary soil (sandy loam) was collected from the top 15- to 20-cm depth on the Long Valley Experimental Forest, approximately 96 km south of Flagstaff, Arizona, at an elevation of 2,230 m. Basalt soil (clay loam) was collected from the same depth on the Fort Valley Experimental Forest, 16 km northwest of Flagstaff. Soils were air-dried for several days then sieved through a 3.2-mm screen.

Trees

Bare-root ponderosa pine seedlings, 2 years old, were raised at the Forest Service nursery at Albuquerque, New Mexico, from seed collected on the Flagstaff Ranger District of the Coconino National Forest. Seeds were sown in May 1982, and seedlings were lifted in late February 1984 and stored at temperatures slightly above freezing until planted.

Container seedlings were raised in the Bureau of Indian Affairs' greenhouse at McNary, Arizona, from seed collected on the North Kaibab Ranger District of the Kaibab National Forest. Seedlings were raised in Tinus Rootrainers[2] (0.41 liter) during the late summer of 1983 and hardened off in a lathhouse over winter. In June 1984, the seedlings were taken to Flagstaff and stored outside until used.

Planting

In June 1984, container and bare-root seedlings were planted in 165- by 330-mm molded fiber pots lined with 0.05-mm polyethylene bags. Trees were planted in pots to a depth of 25 cm. Each pot was saturated with tap water, and the bottom of the bag was perforated to allow drainage. Pots were placed in a greenhouse and kept

[2]*The use of trade and company names is for the benefit of the reader; such use does not constitute an official endorsement or approval of any service or product by the U.S. Department of Agriculture to the exclusion of others that may be suitable.*

well watered until August 6, 1984, when the study began. At the time of study establishment, container seedlings averaged about 20 cm in height and 8.5 mm in diameter at the root collar. Bare-root seedlings were slightly larger, averaging 24 cm in height and 9.5 mm in diameter.

Mean day/night temperatures in the greenhouse and daytime humidities are shown in table 1.

Experimental Design

The experiment consisted of four groups of trees, each group containing four rows of 13 potted seedlings (total 52 pots). Each row was randomly assigned one of the following treatments:

1. Basalt soil, container seedlings.
2. Basalt soil, bare-root seedlings.
3. Sedimentary soil, container seedlings.
4. Sedimentary soil, bare-root seedlings.

Each group of pots was placed in a separate wooden frame on the floor of the greenhouse. Pots were saturated with tap water and allowed to drain for 24 h. Three control pots in each row were watered regularly throughout the course of the experiment. Bags in the other 10 pots in each row were securely fastened to the tree stems with a plastic tie, and the pots were not watered again until after measurements were collected. Three of the 10 stressed pots were then randomly selected for future measurements. The other seven seedlings in each row were monitored for survival.

At the same time that the first groups were prepared, an equal number of potted seedlings were set aside for study in 1985.

Measurements

On October 23, 1984, one group of pots was randomly selected for study. At 0500, 0800, 1100, 1400, 1700 h, transpiration and stomatal conductance of current (new) needles of seedlings were measured with a Li-Cor 1600 porometer. To obtain needle measurements, two fascicles (six needles) attached to the seedlings were placed in the conifer chamber of the porometer. Percentage area of the conifer chamber occupied by the needles was determined and used to adjust E and gs readings. The needle water potential of unstressed and stressed seedlings was determined with a pressure chamber (PMS Instruments, Corvallis, OR) at 0500 and 1400 h, using individual needle fascicles. At least two measurements were collected from each seedling.

At 1400 h we collected soil cores from the 10–15 and 20–25 cm soil depths in stressed pots for SMC determinations. We determined soil water potential from regression equations plotting ψs as determined by thermocouple psychrometer against soil moisture content determined gravimetrically (Heidmann et al. 1990).

After the last porometer measurements were made at 1700 h, all pots were resaturated, then left to drain for 36 h until 0500 h of the second day. Measurements were again obtained from the same seedlings, then the pots were left open and watered regularly until the end of the study. Thereafter the same procedures were repeated on November 6, November 27, and December 19, with separate sets of pots.

For the second experiment conducted in 1985, groups of pots were set up as in 1984. Seedlings had generally completed height growth, but not diameter growth. We randomly selected one of the groups for measurement on July 22, after 61 days of drought.

Because no measurable transpiration had occurred before dawn during the preceding year, porometer readings were taken at 0800, 1100, 1400, and 1700 h. Needle water potential was measured as before, except that predawn measurements were collected at 0400 h.

Measurements were also collected on August 14 and 24 after 84 and 96 days of drought. After initial measurements, pots (control and stressed seedlings) were resaturated and measurements were repeated after a 39-h interval.

Table 1.—Mean monthly day and night temperatures and mean daytime relative humidity in the greenhouse during drought experiments conducted with ponderosa pine seedlings during 1984 and 1985.[1] (s) = standard deviation.

Month	Mean temperature, °C				Mean daytime humidity, %	
	Max.	(s)	Min.	(s)	Mean	(s)
1984						
August	30.2	2.1	17.6	0.9	30.2	6.3
September	31.9	2.1	17.8	1.1	24.0	3.2
October	25.8	1.3	12.3	1.9	28.2	8.7
November	23.5	3.1	10.7	2.5	31.8	8.2
1985						
May	23.4	1.9	12.6	0.8	32.3	4.2
June	26.7	0.4	14.0	0.0	32.0	0.1
July	24.8	2.7	16.7	2.2	45.9	7.1
August	27.3	1.0	18.2	1.1	34.0	3.4

[1]*Computed from weekly means.*

Analysis of Data

Initially, multifactor analysis of variance was used to assess consistency of response associated with treatment (watered and stressed) and stock types (containerized and bare-root) across time for transpiration and conductance rates. Separate analyses were conducted for each soil type. Severe interaction between sample date and treatment was present in the fall data, necessitating separate analyses for each sample data. Interaction between treatment and sample date was only weakly present in the summer basalt data and nonexistent in the sedimentary soil data. Analyses of individual sample dates were consistent for pooled analyses for basalt soil, so time was ignored in the analysis of summer data for both soils. This provided much larger sample sizes and, therefore, better comparisons among treatments. Also, results were extremely consistent between stock types for the summer sedimentary soil data, so only treatments were compared.

For both years, responses were inconsistently variable and nonnormal. Therefore, to avoid violation of assumptions associated with standard analysis of variance, permutation procedures were used to conduct the final set of comparisons (Mielke 1984). In the fall, individual pairwise comparisons between treatment stock combinations were conducted at $\alpha = 0.10$, after first evaluating an overall test of differences at $\alpha = 0.05$. This was judged a reasonable compromise, because $p = 0.05$ was the smallest significance level attainable for the small sample sizes associated with individual comparisons. During the summer, because interaction was either quite weak or nonexistent, data were pooled across time for analyses and both overall tests and individual comparisons were evaluated at $\alpha = 0.05$.

Statistical differences in needle water potential by time of day, soil, planting stock, and treatments were determined by repeated measures analysis of variance considering time of day a repeated measurement, with computations executed using the manova procedure of SPSS-PC+ (Norusis 1988). Significant interaction was generally present between time of day and one or more factors, necessitating separate analyses for each time.

Results

Transpiration

Differences in transpiration during the fall were related to time of day and length of time from inception of study for soil/stock combinations. Seedlings, in general, reached maximum E rates between 1100 and 1400 h. Before rewatering, unwatered (stressed) seedlings transpired at a much lower rate than watered seedlings (fig. 1). After rewatering, rates were somewhat lower for

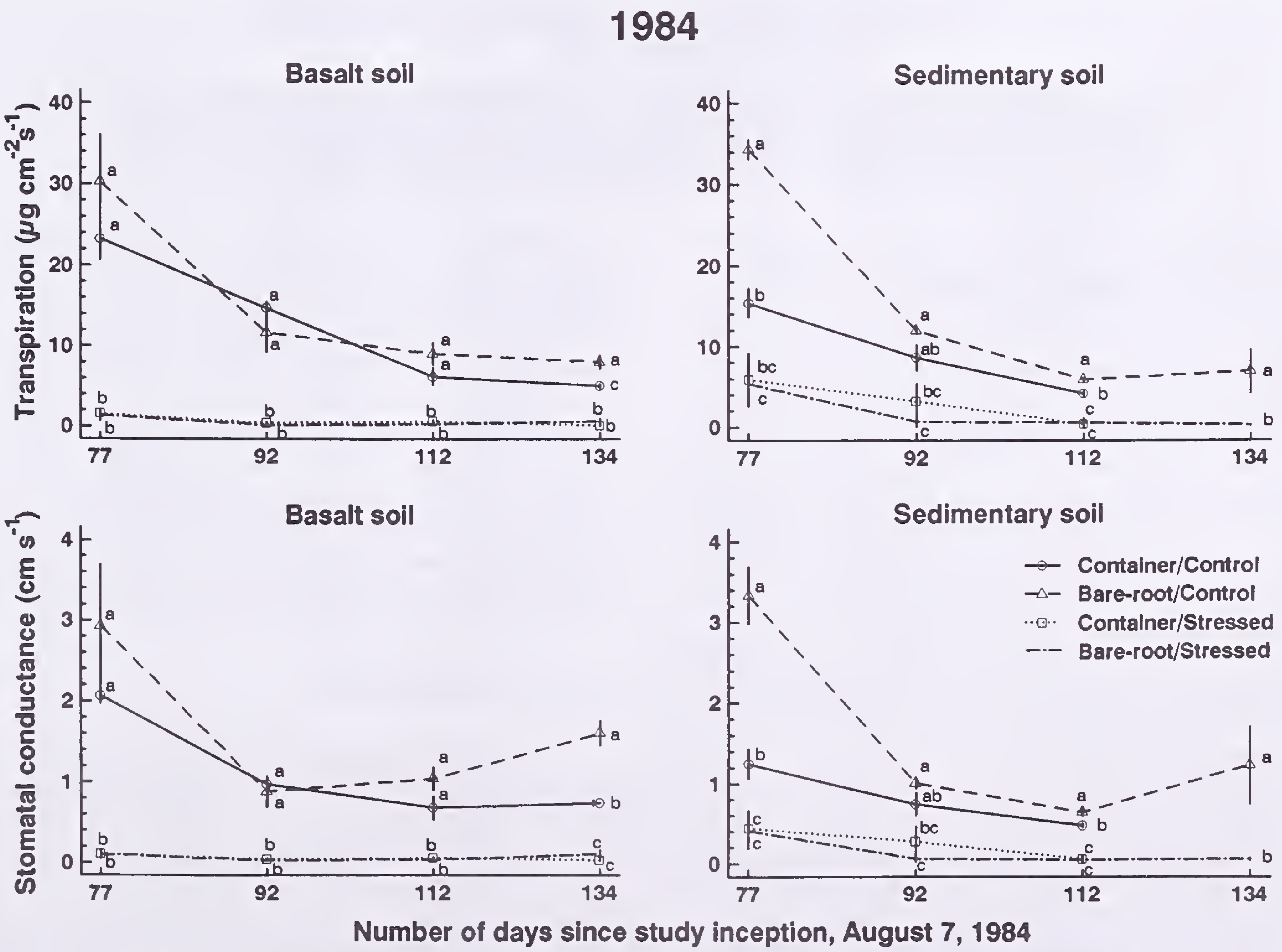

Figure 1.—Maximum daily transpiration (E) and stomatal conductance (gs) rates of watered and unwatered ponderosa pine seedlings growing in two soils, 1984. Vertical bars indicate standard errors. For a particular date, soil/stock combinations with different letters are significantly different ($\alpha = 0.10$) according to permutation test procedures (Mielke 1984).

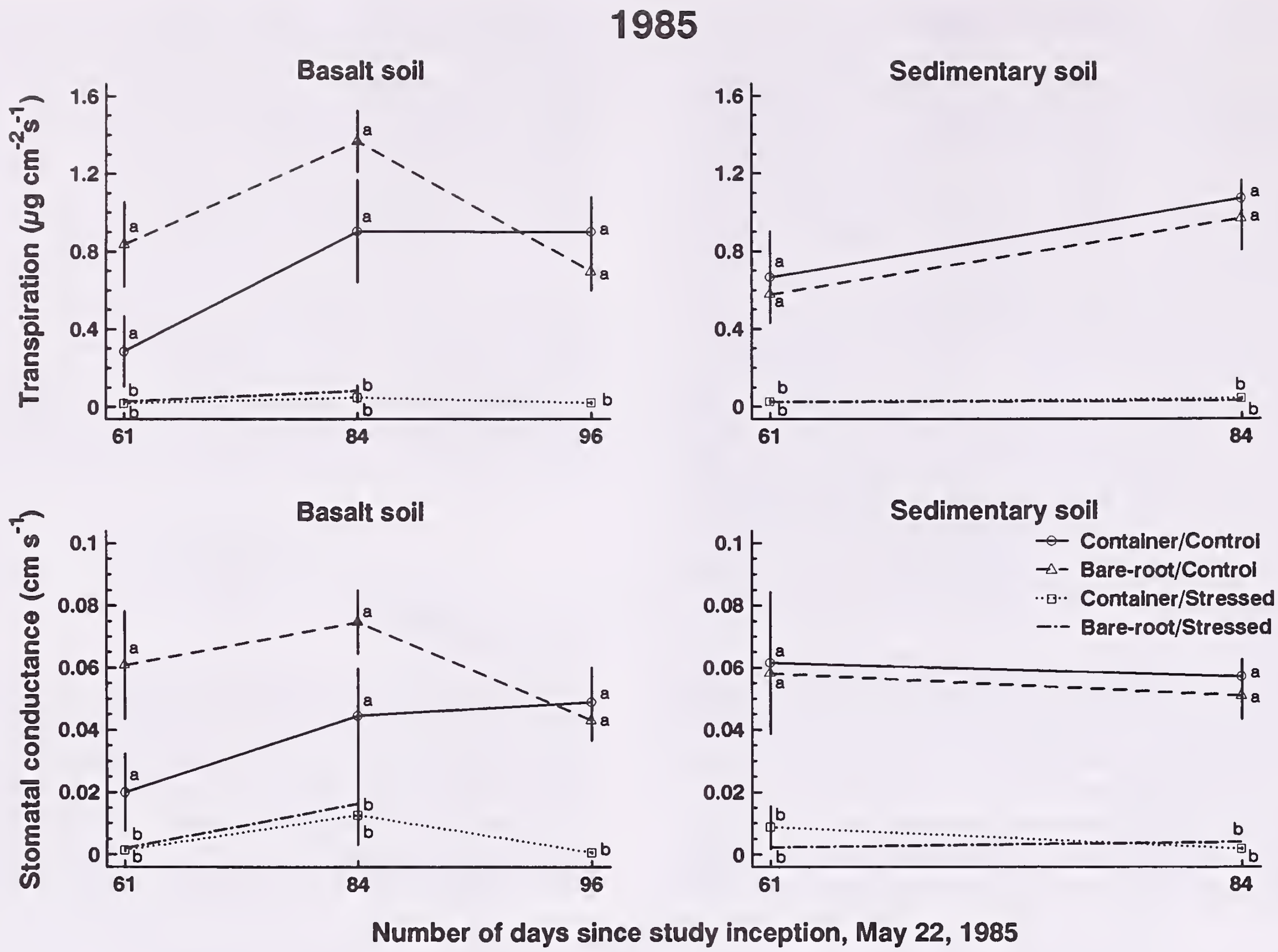

Figure 2.—Maximum daily transpiration (E) and stomatal conductance (gs) rates of watered and unwatered ponderosa pine seedlings growing in two soils, 1985. Vertical bars indicate standard errors. For a particular date, soil/stock combinations with different letters are significantly different ($\alpha = 0.05$) according to permutation test procedures (Mielke 1984).

stressed seedlings. Transpiration rates of watered seedlings declined throughout the fall and were generally at low levels in mid-December after 112 days (fig. 1). Throughout the fall there was no difference in E between container and bare-root watered seedlings on basalt soil until after 134 days, while on sedimentary soil there was a difference ($p = 0.10$) for all time periods except after 92 days. On basalt soil E rates of container and bare-root stressed seedlings were not different from each other but were significantly lower than for watered seedlings. On sedimentary soil, however, E rates of watered and stressed container seedlings were not different until after 112 days in November (fig. 1, $p = 0.10$).

During the fall there was no mortality of watered or stressed seedlings. Because we had no container seedlings in sedimentary soil available for sampling, those values are missing in figure 1.

Results from the summer were quite different than those in the fall. Daily transpiration patterns were similar but maximum rates were considerably lower. In addition, there was a tendency for E rates of watered seedlings to rise over time during the summer (fig. 2). Maximum E rates of bare-root seedlings in the fall on basalt soil were over 30 $\mu g\ cm^{-2}\ s^{-1}$ compared to slightly over 1 $\mu g\ cm^{-2}\ s^{-1}$ in the summer (figs. 1, 2). After 61 days of drought during the summer, watered container and bare-root seedlings on both soils had significantly higher E rates than stressed seedlings ($p = 0.05$). There was no difference in E between bare-root and container seedlings by watering treatment on either soil; although there appear to be differences for basalt soil, results were too variable to be significant (fig. 2, $p = 0.05$). Transpiration of stressed seedlings was almost identical for both stock types on both soils (fig. 2).

There was no mortality of watered seedlings during the summer. Survival of stressed container and bare-root seedlings, however, was 60% for each stock type on basalt soil while on sedimentary soil survival was 20% and 10% respectively.

Stomatal Conductance

As might be expected, stomatal conductance patterns in the fall paralleled transpiration patterns (fig. 1). Conductance of watered needles usually reached a maximum between 1100 and 1400 h. Maximum gs of watered seedlings generally declined throughout the fall (fig. 1). Watered seedlings on basalt soil had a significantly greater gs than stressed seedlings ($p = 0.10$). There were no differences in gs for container and bare-root seedlings on basalt soil within watering treatments until December 19 (134 days) when gs of watered bare-root seedlings

was greater than watered container seedlings and both were significantly greater than stressed seedlings ($p = 0.10$). Conductance of watered bare-root seedlings began to rise after 92 days (fig. 1).

The picture on sedimentary soil is less clear. Throughout the fall, watered bare-root seedlings had a greater gs than watered container seedlings, and both types of watered seedlings had greater gs rates than stressed seedlings except after 92 days (fig. 1, $p = 0.10$). After rewatering, gs of stressed seedlings rose, but only to about 50% that of watered seedlings.

During the summer, conductance patterns were also similar to transpiration patterns (fig. 2). Although there appears to be a difference between container and bare-root watered seedlings on basalt soil, results were too variable to be significant ($p = 0.05$). Conductance of watered seedlings, however, was greater than stressed seedlings ($p = 0.05$). On sedimentary soil, differences existed between watering treatments but not between stock types ($p = 0.05$).

Needle Water Potential

After 112 days of drought in the fall, there were highly significant differences in needle water potential between watering treatments overall, and at 0500 and 1400 h ($p < 0.00$). There was no difference in $\psi\ell$ of stressed seedlings by time of day ($p = 0.927$). Control seedlings, however, had a $\psi\ell$ of –0.31 MPa at 0500 h that dropped to –1.27 MPa at 1400 h ($p < 0.00$). There were no differences between soils or planting stock at either time.

After rewatering, $\psi\ell$ of stressed seedlings rose to levels similar to those for watered seedlings (fig. 3). Overall, there was no difference between watered and stressed seedlings.

Results after an 85-day summer drought were similar to those from the fall of 1984, except that $\psi\ell$ of stressed seedlings was considerably lower (fig. 4). Several seedlings had a $\psi\ell$ of –6.2 MPa. There were large differences between watered and stressed seedlings overall, and at 0400 and 1400 h ($p = 0.000$). There were no differences between soils or planting stock except for container and bare-root seedlings at 1400 h ($p = 0.044$, table 2). After rewatering, the only differences were between watered and stressed seedlings at 0400 h ($p = 0.007$). However, significant interactions clouded comparisons of planting stock after rewatering at 0400 h; separate comparisons of planting stock for each watering treatment were nonsignificant ($p < 0.29$). At 1400 h, separate comparisons of planting stock for each soil revealed no differences for basalt soil ($p = 0.45$), but lower $\psi\ell$ for bare-root seedlings (–1.8 vs. –1.4 MPa) for sedimentary soils ($p = 0.02$). Watered and stressed seedling needle potentials were different by time of day both before and after rewatering ($p = 0.001$).

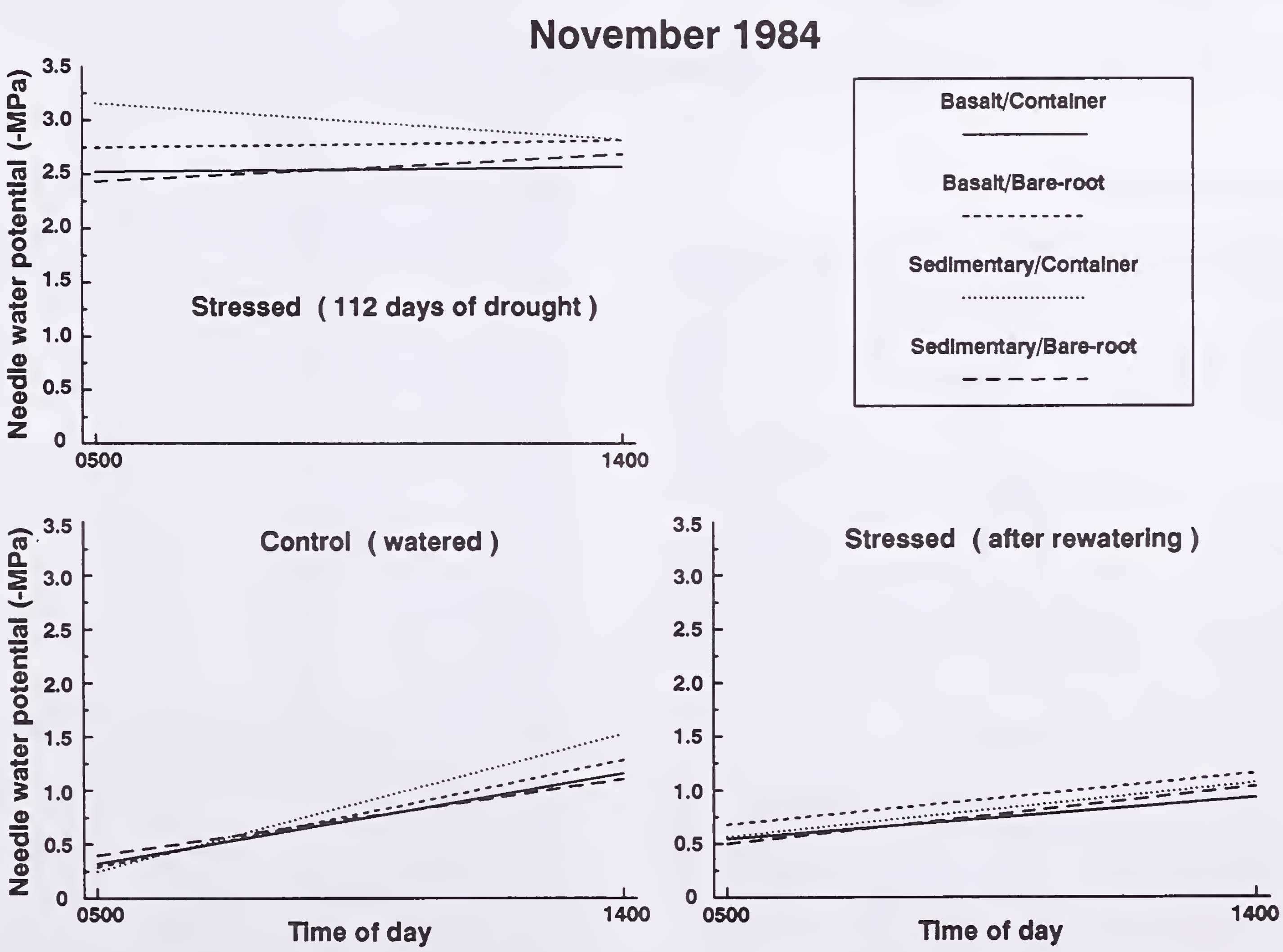

Figure 3.—Needle water potential of watered and unwatered ponderosa pine seedlings, November 1984.

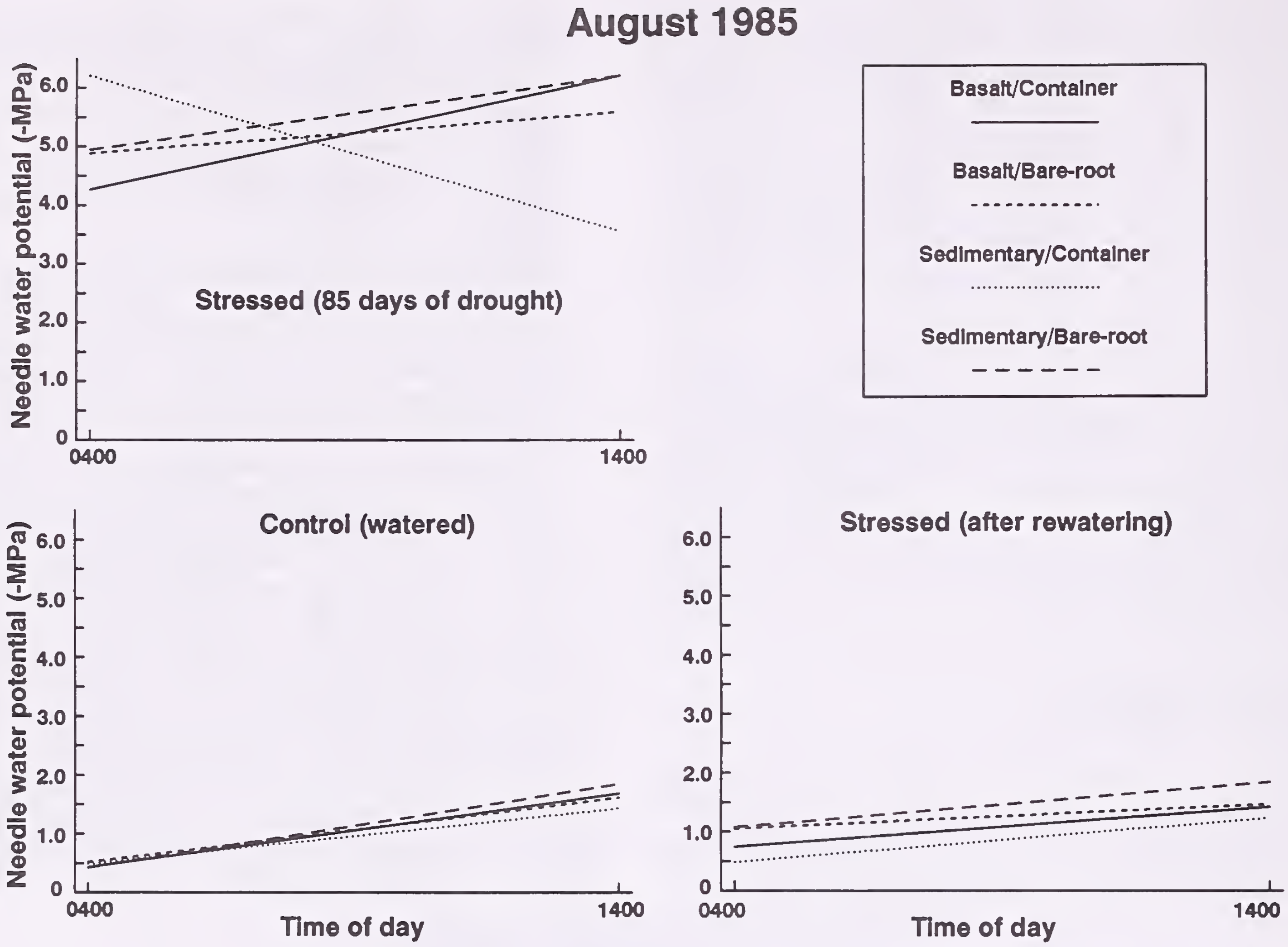

Figure 4.—Needle water potential of watered and unwatered ponderosa pine seedlings, August 1985.

Soil Water Potential

After 112 days of drought in the fall 1984, SMC averaged 11.34% in basalt soil with corresponding soil water potential of –1.68 MPa. In sedimentary soil, SMC was 2.48 with ψs of –0.18 MPa. After the summer drought, however, SMC of basalt soil averaged 9.6% in pots with live trees (ψs –3.16 MPa). Only one sampled seedling was dead in basalt soil. In this pot SMC was 9.44% with ψs of –3.50 MPa. In sedimentary soil, pots with live seedlings had a SMC of 1.35% and a mean ψs –2.77 MPa. Soil moisture content in four pots with dead seedlings averaged 1.43% with ψs of –2.41 MPa. In sedimentary soil, ψs at the 10–15 cm depth was considerably lower than at the 20–25 cm depth (–3.37 MPa vs. –2.20 MPa) for pots with live seedlings.

Discussion

Ponderosa pine seedlings appear to endure long periods of drought by slowing down physiological processes. Stomata close and transpiration is reduced to low levels. In addition, Heidmann (unpublished) has recently found dramatic reductions in net photosynthetic rates (Pn) after prolonged water stress.

Upon rewatering, seedlings recover rapidly. Transpiration and needle water potential approach rates for well-watered controls within a day and a half, but stomatal conductance recovers less rapidly.

There were differences in seedling response by the time of year. This may have been due to dormancy status or the fact that seedlings during the summer were larger since they had grown for one more season. Well-watered seedlings in the fall had greater transpiration and conductance rates than in the summer. Although rates were high in the early fall, they declined over time, reaching a minimum in December. Andersson (1980) found that transpiration rates in Scots pine (*Pinus sylvestris* L.) seedlings in the greenhouse declined with decreasing daylength and temperature. In loblolly pine (*Pinus taeda* L.) transpiration and conductance also tended to decline with decreasing temperature (Teskey et al. 1986).

Although our rates were lower during the summer, total water use was probably greater. This is because of longer daylength during the summer during which stomata would be open for a longer period of time. In addition, larger seedlings during the summer would have a greater transpiring needle surface. Heidmann (unpublished), in studies currently being conducted, has determined that under conditions similar to those described here, stressed seedlings during the summer utilize about 39% more water than stressed seedlings during the fall.

Our seedlings were still transpiring some water after long periods of drought. In this respect, they are different from some other conifers. For example, after only 9 days of soil drying, in jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill) BSP) transpiration dropped to 0% of the control, and in white spruce (*Picea glauca* (Moench) Voss), transpiration dropped to 53% of the control (Roberts and Dumbroff 1986).

Roberts and Dumbroff (1986) suggest that drought resistance of jack pine is related to sensitivity of stomata to a small increase in endogenous abscisic acid (ABA) concentration above a high basal level and to a prolonged "aftereffect." We did not measure ABA concentration in this study, but conductance of stressed seedlings was approximately half that of controls 42 h after rewatering, indicating the presence of an aftereffect. In addition, we know from experiments recently concluded that ABA levels of new needles of stressed ponderosa pine seedlings are more than six times that of watered control seedlings. We also found transpiration and conductance rates of stressed seedlings to be 14.7% and 11.5% that of watered controls (Heidmann, unpublished).

Differences in water use by season are corroborated by needle and soil water potential values. After a fall drought $\psi\ell$ values were about half those recorded after the summer drought. Some stressed seedlings during the summer endured $\psi\ell$ of –6.2 MPa and recovered. Our results are lower than those reported previously for ponderosa pine. Rietveld (unpublished), for example, determined that $\psi\ell$ in the range of –2.0 to –2.5 MPa was the maximum that southwestern ponderosa pine seedlings in the field could endure over a sustained period. Working with ponderosa pine seedlings, Petersen and Maxwell (1987) found that predawn $\psi\ell$ ranged from –0.5 MPa when foliage from competing plants was essentially absent to less than 3.0 when foliage was more extensive. Seedlings with $\psi\ell$ of –6.0 MPa were dead. Heth and Kramer (1975) found that loblolly pine (*Pinus taeda* L.) survived at $\psi\ell$ values close to –4.0 MPa.

In the early stages of drought, needle water potential values are high before dawn, dropping to low levels during midday. When drought occurs over a prolonged period, $\psi\ell$ are low throughout the day. According to Waring and Running (1976), a water deficit will develop during the day whenever the rate of transpiration exceeds the recharge from the soil root zone and sapwood. If transpiration ceases at night and water available in the root zone exceeds 20% of soil water-holding capacity, then complete recharge will occur sometime during the night. When soil moisture is less than 20% of capacity, water uptake from the soil will be reduced exponentially to zero when all available root zone water is exhausted.

Soil water potential values were also considerably higher in the fall than during the summer. Even after a 112-day drought period, ψs of sedimentary soil was about 14 times greater than after a summer drought. This is reflected by the fact that there was no mortality after a fall drought, but considerable mortality after a drought during the summer. These results imply that seedlings may be planted successfully in the fall. This has been true for container seedlings, but fall planting of bare-root seedlings has not been successful, perhaps because their smaller root systems may not be able to absorb the water necessary to replenish that being lost by the crowns.

From our results it appears that ponderosa pine seedlings would have difficulty surviving in basalt soils when soil water potential drops below –3.4 MPa (9.5% SMC). This is about 27% of the soil's field capacity (water-holding capacity). In sedimentary soils, individual seedlings survived when ψs was as low as –3.6 MPa. A more realistic figure, however, probably lies between –1.43 and –3.34 MPa (1.25% to 1.50% SMC). Soil moisture contents at these values are 12.8% and 15.3% of field capacity. Thus, our results are somewhat different from those of Waring and Running (1976).

In these experiments there was little difference in performance between container and bare-root seedlings. There were differences, however, between soil types. Survival was greater on basalt soil. This can probably be correlated with the greater moisture-holding capacity of these soils. Therefore, it appears contradictory that in the field natural regeneration of ponderosa pine is much easier to obtain on sedimentary soils. As mentioned previously, however, this is most likely explained by the fact that on basalt soils 1-year-old seedlings are quite small and frost heave at excessive rates. On sedimentary soils, seedlings are much larger and frost heaving is less severe (Heidmann 1975).

Ponderosa pine seedlings, container or bare-root, may be successfully planted on basalt or sedimentary soils. The results of these experiments indicate, however, that in cases of severe drought, survival will probably be lower on sedimentary soils.

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Keywords: Stomatal conductance, transpiration, *Pinus ponderosa*, drought, needle water potential

U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

Rocky Mountains

Southwest

Great Plains

The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

RESEARCH FOCUS

Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

RESEARCH LOCATIONS

Research Work Units of the Rocky Mountain Station are operated in cooperation with universities in the following cities:

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Flagstaff, Arizona
Fort Collins, Colorado*
Laramie, Wyoming
Lincoln, Nebraska
Rapid City, South Dakota
Tempe, Arizona

*Station Headquarters: 240 W. Prospect Rd., Fort Collins, CO 80526